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Coccolithophorids in Polar Waters: *Trigonaspis* spp. Revisited

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Abstract. A group of weakly calcified coccolithophorid genera and species were described from polar regions several decades ago. In the interim period a few additional findings have been reported adding to the morphological and biogeographical databases of some of the species. The holococcolithophorid genus *Trigonaspis* is revisited here with the purpose of providing, based on additional sampling from both polar regions, an update on species morphology, life history aspects and biogeography. The genus *Trigonaspis* as currently circumscribed comprises four taxa – two from each polar region. The triangular plates of crystallites that cover the surfaces of both the tower-shaped flagellar pole coccoliths and the disc-shaped body coccoliths are the keystone features of the genus. Circumstantial evidence exists linking species of *Trigonaspis* with species of *Pappomonas* in haploid-diploid life cycles.

Key words: Coccolithophorid, holococcolith, *Trigonaspis*, polar regions, electron microscopy.

Abbreviations: TEM – transmission electron microscope; SEM – scanning electron microscope; LM – light microscope; FPC – flagellar pole coccolith; BC – body coccolith; AMERIEZ, EPOS, ANT X/3, NBP – acronyms for Antarctic cruises (see Materials and Methods); NEW, NOW – acronyms for Arctic cruises (see Materials and Methods); AS – Arctic Station.

INTRODUCTION

A diverse assemblage of weakly calcified coccolithophorids (Haptophyta) was persistently present at high latitude sampling sites during investigations using transmission electron microscopical techniques to survey an area of interest (Manton and Oates 1975; Manton and Sutherland 1975; Manton *et al.* 1976a, b, 1977; Thomsen 1980a, b, c, d, 1981; Thomsen *et al.*

1988, 1991; Thomsen *et al.* 2013, Thomsen and Østergaard 2014a, b). A core group of heterococcolithophorid genera, viz. *Papposphaera* Tangen 1972, *Pappomonas* Manton and Oates 1975, *Wigwamma* Manton *et al.* 1977, and a second array of holococcolithophorid genera, viz. *Turrisphaera* Manton *et al.* 1976b, *Calciarcus* Manton *et al.* 1977, *Trigonaspis* Thomsen 1980a, and *Quaternariella* Thomsen 1980d, were established to accommodate the more than 20 species that have been identified so far. Irrespective of the generic affiliation these taxa share basic morphological and physiological features such as modest cell dimensions (3–5 µm in diam.), weakly calcified coccoliths, and an aplastic condition. The fact that these organisms, across

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the entire range of bipolar genera and species, all rely exclusively on heterotrophy (most likely scavenging bacteria) immediately distinguishes this cluster of taxa from the remaining coccolithophorids that are known to be photosynthetic organisms, albeit in many cases and dependent on environmental pressures with a possibility, at least within the flagellated life cycle stages, of switching to mixotrophy (Parke and Adams 1960; Klaveness 1973; Houdan *et al.* 2006). A key question to be addressed in the future is whether the physiological and biogeographical homogeneity of this cluster of organisms is also reflected in a phylogenetic isolation of the group from the remaining coccolithophorids. According to the chromalveolate hypothesis the four eukaryotic groups with chlorophyll *c* containing plastids originate from a single photosynthetic ancestor, which acquired its plastids by secondary endosymbiosis with a red alga. However, as emphasized by Bourain *et al.* (2010) molecular phylogenies have so far failed to either support or disprove this view. These authors in fact argue in favor of more complex evolutionary scenarios involving multiple higher order eukaryote–eukaryote endosymbiosis, which leaves from our perspective room for accepting a heterotrophic starting point for the haptophyte lineage and the possibility of placing the polar non-photosynthetic forms in a keystone phylogenetic position within the haptophyte tree. Also Liu *et al.* (2010) concludes that we cannot rule out the possibility that the haptophytes led an early heterotrophic life before acquiring their plastid. The contrasting evolutionary scenario with respect to the polar lightly calcified coccolithophorids involves a secondary loss of the photosynthetic apparatus in response to the low light regime encountered when they expanded into high latitude regions.

We are currently in the process of preparing a series of papers that in turn updates our knowledge on each of the bipolar genera (Thomsen *et al.* 2013; Thomsen and Østergaard 2014a, b). Since the first description of these taxa that dates back three decades or more, very little additional information has been acquired. However, we are fortunate enough to have access to fairly vast sources of TEM material that stem from collection efforts conducted mostly during the nineties, and on top of that recent and still ongoing sampling programs conducted in e.g. the fiord systems of the high arctic Svalbard that utilizes a ‘state of the art’ SEM to analyze the material collected.

In this paper we examine species of the holococcolithophorid genus *Trigonaspis* Thomsen 1980a.

MATERIALS AND METHODS

For the purpose of this paper we have with regard to the Southern Ocean considered material sampled from south of the Antarctic Convergence and in the northern hemisphere the Arctic Ocean and its surrounding ice-covered seas.

The Arctic material originates from the R/V ‘Polarstern’ ARK IX/3 North-East Water Polynya (NEW) cruise June–July 1993 and the R/V ‘Pierre Radisson’ North Water Polynya cruise (NOW) April–May 1998 (Fig. 1). Additional northern hemisphere sampling took place at the University of Copenhagen Arctic Station (Disko Bay, West Greenland) during the summers of 1988, 1990 and 1994 (Fig. 1).

The Antarctic material originates from the R/V ‘Melville’ AMERIEZ cruise (March 1986), the R/V ‘Polarstern’ ANT VII/3 ‘EPOS II’ cruise (Nov. 1988 – Jan. 1989) and the R/V ‘Polarstern’ ANT X/3 ‘Herbst im Eis’ cruise (April–May 1992), with all cruises occupying stations in the Weddell Sea region (Fig. 2). Additional sampling took place in the Ross Sea on board the R/V Nathaniel B Palmer (Jan.–Feb. 1999 / NBP 99-01 Ice Cruise).

The protocol for processing water samples for transmission electron microscopy and light microscopy were similar on all sampling occasions (see Thomsen *et al.* 2013 for further details).

RESULTS

Trigonaspis Thomsen 1980a

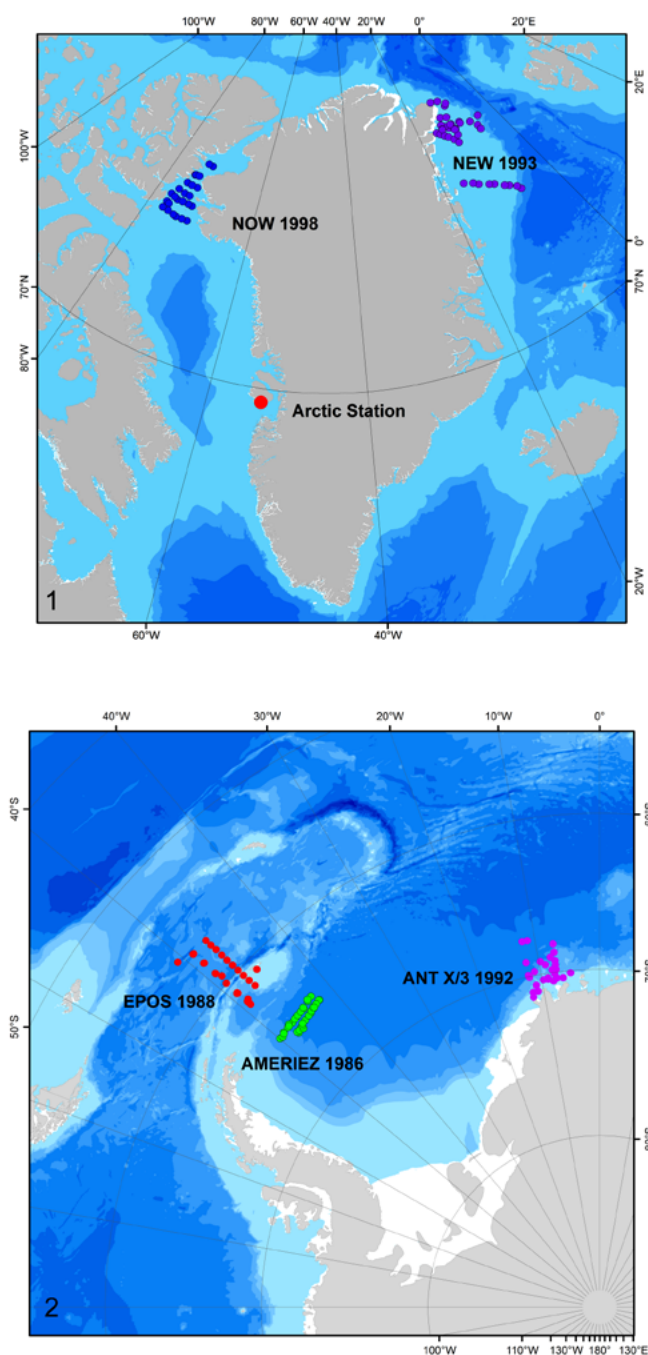
The original description of this holococcolithophorid genus as reproduced below was based on material from West Greenland:

Small biflagellate coccolithophorids with a short haptonema. Periplast composed of coccoliths which are tower-like near the flagellar pole. Coccolith crystallites small triangular plates composed of three subunits. Small organic scales, always unmineralized, appear below the coccolith base-plates.

Type species: Trigonaspis diskoensis

The key characteristics are dimorphic (occasionally varimorphic) coccoliths that involves a tuft of tower-shaped coccoliths encircling the flagellar pole, and above all the monolayer of triangular crystallite groups that cover all coccolith surfaces.

The most closely related genus is *Turrisphaera* Manton *et al.* 1976b which is distinguished from *Trigonaspis* based on the presence of hexangular rather than triangular crystallite groups. Circumstantial evidence in support of this distinction has subsequently come from the discovery of combination cells (Thomsen *et al.* 1991) where *Papposphaera* spp. share a common life history with *Turrisphaera* spp., while species of *Trigo-*



Figs 1–2. Collection sites. **1** – map of the Arctic (Greenland) indicating sampling sites; **2** – map of the Antarctic (Weddell Sea) showing the location of sampling sites.

naspis interact with species of *Pappomonas* (see also Thomsen and Østergaard 2014b).

Three species of *Trigonaspis*, viz. *T. diskoensis* Thomsen, 1980a, *T. minutissima* Thomsen, 1980a and

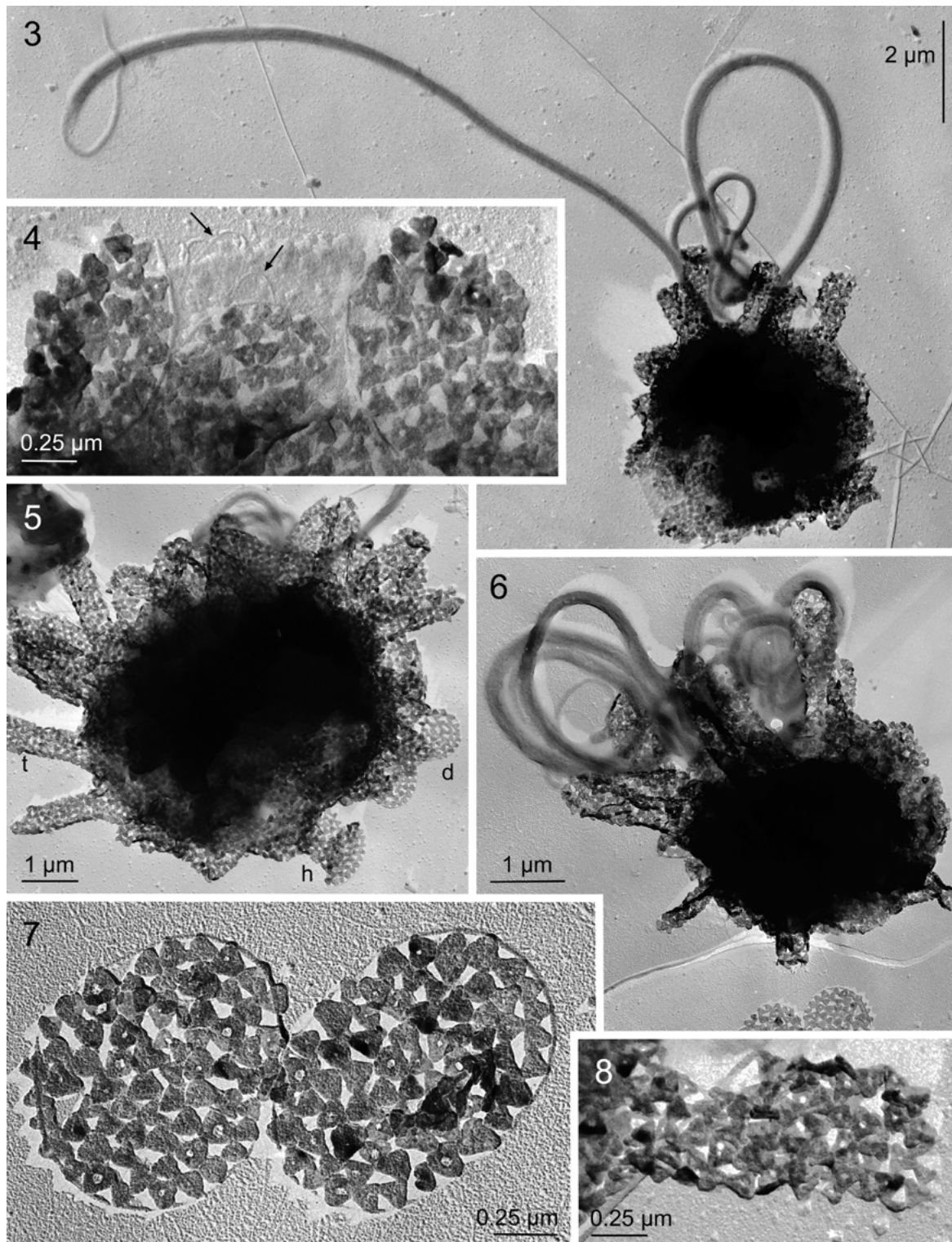
T. melvillea Thomsen in Thomsen *et al.* (1988) have been described so far. A fourth species (*Pappomonas garrisonii* HOL = *Trigonaspis* sp.) is illustrated and discussed here based on material from the Antarctic.

Trigonaspis diskoensis Thomsen 1980a

Trigonaspis diskoensis has so far been recorded only from the type locality in Disko Bay, West Greenland (Thomsen 1980a; Hansen *et al.* 1988; Østergaard 1993; Clausen *et al.* 1994). Here we have the opportunity to reexamine the species based on extensive material from NE Greenland (NEW).

The general appearance of the cell including appendages and the coccolith coverage is accounted for in Figs 3, 5, 6, while numerical facts have been assembled in Table 1. Tower-shaped flagellar pole coccoliths, 4–7 in number, form a corona at the anterior pole (Figs 3, 6, 11). The typical flagellar pole coccolith (FPC) has a base, c. 1 μm wide, that supports a tower-like structure which is fairly narrow in the middle (c. 0.5 μm), while slightly widened towards the distal end (Fig. 8). In more general terms the FPC can be described as an asymmetrically double-flared tube. At the antapical pole the coccolith coverage comprises disc-shaped oval organic plates (Figs 3, 4, 6, 7) supporting a monolayer of triangular groups of crystallites. In between these two extremes there appears to be a more or less gradual transition in coccolith shapes, involving e.g. ‘hat-shaped’ forms (Fig. 10), characterized by different degrees of elevation of the central part of the coccolith, occurring in an equatorial band around the cell. It is thus evident that *T. diskoensis* is not strictly dimorphic but rather varimorphic.

Triangular groups of crystallites are shown at high magnification in Figs 4, 7–10. In the flagellar pole coccoliths the triangles appear to be organized in a single-layered helical pattern where one turn occupies 8–10 triangles (Fig. 9). The monolayer of triangles on the flattened body coccoliths (BC) also displays clear elements of a basic symmetrical layout involving the deposition of triangles in concentric ovals while maintaining a fairly distinct triangular matrix (Figs 4 and 7). The individual triangle, irrespective of coming from a tower-shaped or a flat coccolith, is characterized by rounded to semi-pointed corners and straight or slightly concave edges. It must be emphasized that decalcification, whether natural or accidental and caused by e.g. preparational procedures, will impact on the shape and appearance of the triangular groups of crystallites. We thus interpret the tiny central hole seen in numerous tri-



Figs 3–8. *Trigonaspis diskoensis*. TEM whole mounts from NE Greenland (NEW). **3** – whole cell with flagella and a curled up haptonema. Tower-shaped large coccoliths encircle the flagellar pole; **4** – body coccoliths (detail from Fig. 3) with triangular crystallites arranged in a single layer on top of the visibly rimmed organic base plate. Unmineralized under layer scales are pointed out; **5** – complete cell displaying a range of coccolith shapes, viz. tower-shaped (t), hat-shaped (h) and flat discs (d); **6** – complete cell with appendages and a distinct tuft of tower-shaped flagellar pole coccoliths; **7** – high magnification of flat body coccoliths from the cell shown in Fig. 6; **8** – detail of flagellar pole coccolith from the cell shown in Fig. 3.

Table 1. Cell and coccolith dimensions of *Trigonaspis* spp. Notice that none of the measurements, e.g. cell diam., have been corrected for the transformation from a 3D to a 2D object that occurs to a variable degree during cell drying.

	Flagella	Haplo- nema	Cell diam.	Flagellar pole coccolith (FPC)				Body coccolith (BC)				Size (edge) of triangular plate					Underlayer scales	Source of material	
				Length	Diam. prox.	Diam. dist.	Diam. min.	Number	Length	Width	Elev. above base-plate	Triang. plates per scale	Range	Mean	SD	min/max	n		
<i>T. diskoensis</i>																			
Thomsen 1980a	15–19.2/ c.13	8–10	4.7–5.6	1.7–2.5	0.6–1.0		0.3–0.4	4–5 (7)	0.9–1.5	0.7–1.0	max. 1		0.13–0.16					0.35–0.45 x 0.2–0.25	W. Greenland (Arctic St.) 1977
	19		2.5–4.8	1.8–2.0		0.6–0.7	0.4–0.5	5–7	1–1.25	0.7–0.9		35–70		0.127	0.012	0.107/0.152	34	0.4 x 0.2	NEW (Figs 3–9)
														0.129	0.011	0.096/0.152	49		NEW Fig. 7 (BC)
														0.131	0.014	0.104/0.162	49		NEW Fig. 5 (FPC)
														0.151	0.011	0.13/0.174	16		NEW Fig. 5 (BC)
														0.143	0.014	0.111/0.168	19		NEW40255 (FPC)
	16.4/14.3	9.5	2.6	2		0.45	0.3–0.4	c.6						0.136	0.01	0.12/0.155	16		NEW 40255 (BC)
														0.163	0.012	0.141/0.186	8		AS Fig. 11 (FPC)
																			AS Fig. 10 (intern. coc.)
<i>T. minutissima</i>																			
Thomsen 1980a	13.1–18.5/ 10.2–16.1	c.11	2–3.6	1–1.5	0.3–0.4		0.15–0.25	< 10	0.6–0.75	0.4–0.55			0.08–0.17					0.25 x 0.15	W. Greenland (Arctic St.) 1977
			3.1	1.5										0.117	0.012	0.1/0.135	25		AS 1993 JBO13707 (FPC)
			2.3	1.4–1.5		0.3–0.4	0.16–0.18		0.7–0.8	0.5–0.6		c.25		0.129	0.017	0.09/0.16	28		AS 1993 JBO13707 (BC)
														0.111	0.011	0.09/0.133	45		AS 1993 Fig. 13 (FPC)
														0.133	0.03	0.104/0.151	14		AS 1993 Fig. 14 (BC)
	10.7/10		2.1	1.6		0.35–0.4	0.15–0.2	c.8						0.123	0.014	0.108/0.145	23		AS 1994 Figs 15–16 (FPC)
														0.153	0.007	0.143/0.161	5		AS 1994 Figs 15–16 (BC)
<i>T. melvillea</i>																			
Thomsen <i>et al.</i> 1988	12.4/16.3; 14.9/16.1		3.2–4.4	2–2.3	c.1	0.8–1	0.17–0.23	c.10	0.6–0.8	0.5–0.6			0.11–0.15					0.25–0.37 x 0.18–0.23	Weddell Sea, Antarctica
	21/16.9; 24.4/19.7	13	3.5; 3.6	1.65–1.95				0.9	0.6			c.35							EPOS Figs 19–23
							9							0.104	0.008	0.096/0.115	12		AM Fig. 21 (FPC)
														0.111	0.011	0.092/0.139	20		AM Fig. 22 (BC)
			3.5	1.8				0.8–0.9	0.5–0.6					0.101	0.009	0.082/1.21	38		EPOS 4896 (FPC)
														0.097	0.009	0.08–0.115	14		EPOS 4896 (BC)
<i>P. garrisoni</i> /HOL (= <i>Trig. sp.</i>)																			
			5.3	1.3–3.3										0.174	0.015	0.149/0.195	45		EPOS Figs 24–26
														0.168	0.014	0.138/0.2	33		ANTX/3 21384
<i>Trig./comb (P. garis.)</i>														0.159	0.02	0.115/0.22	56		AM 798
														0.152	0.02	0.125/0.202	17		

angles as a light spot (e.g. Figs 4 and 7) as a phenomenon caused by dissolution. There is little variation in size among triangles from either end of a single coccosphere when measured as the length of the edge (see Table 1). However, slight variability does occur when comparing triangle dimensions across several specimens. The overall range in mean value is in *T. diskoensis* from 0.13–0.16 µm with a standard deviation typically one tenth of the mean value (see Table 1). We are still inclined to believe that the interpretation of a triangle being formed by three calcite rhombohedral crystallites (Thomsen 1980a) is correct. The texture and shadowing of the surface of an individual triangle (see e.g. Figs 4 and 9) often indicates a tripartition of the unit.

Organic under layer scales are visible in places where coccoliths become separated (Fig. 4).

A shared life cycle between the holococcolithophorid *T. diskoensis* and the heterococcolithophorid *Pappomonas borealis* (Manton, Sutherland and McCully 1976a) Thomsen in Thomsen and Østergaard 2014b, has been reported previously (Thomsen *et al.* 1991; Thomsen and Østergaard 2014b).

Biogeographical data on *T. diskoensis* is presented in Table 2.

Trigonaspis minutissima Thomsen 1980a

Trigonaspis minutissima was described alongside the type species of the genus from West Greenland coastal waters (Thomsen 1980a). Subsequent sampling excursions to the same Disko Bay site has on more occasions yielded additional material of *T. minutissima* that allows a reexamination of the taxon.

The appearance of the whole cell including appendages and the overall distribution of coccoliths is accounted for in Figs 12 and 16. Numerical facts have been assembled in Table 1. The tiny cell (Fig. 12) carries a corona of slender and tower-shaped flagellar pole coccoliths while the remaining part of the cell appears to be covered by fairly identical disc-shaped and oval body coccoliths. *Trigonaspis minutissima* in contrast to *T. diskoensis* thus appears to be strictly dimorphic. The slender individual FPC is in principle still a double-flared tube (Figs 13 and 15). The triangular groups of crystallites in this species also appear to be organized in a helical pattern. A single

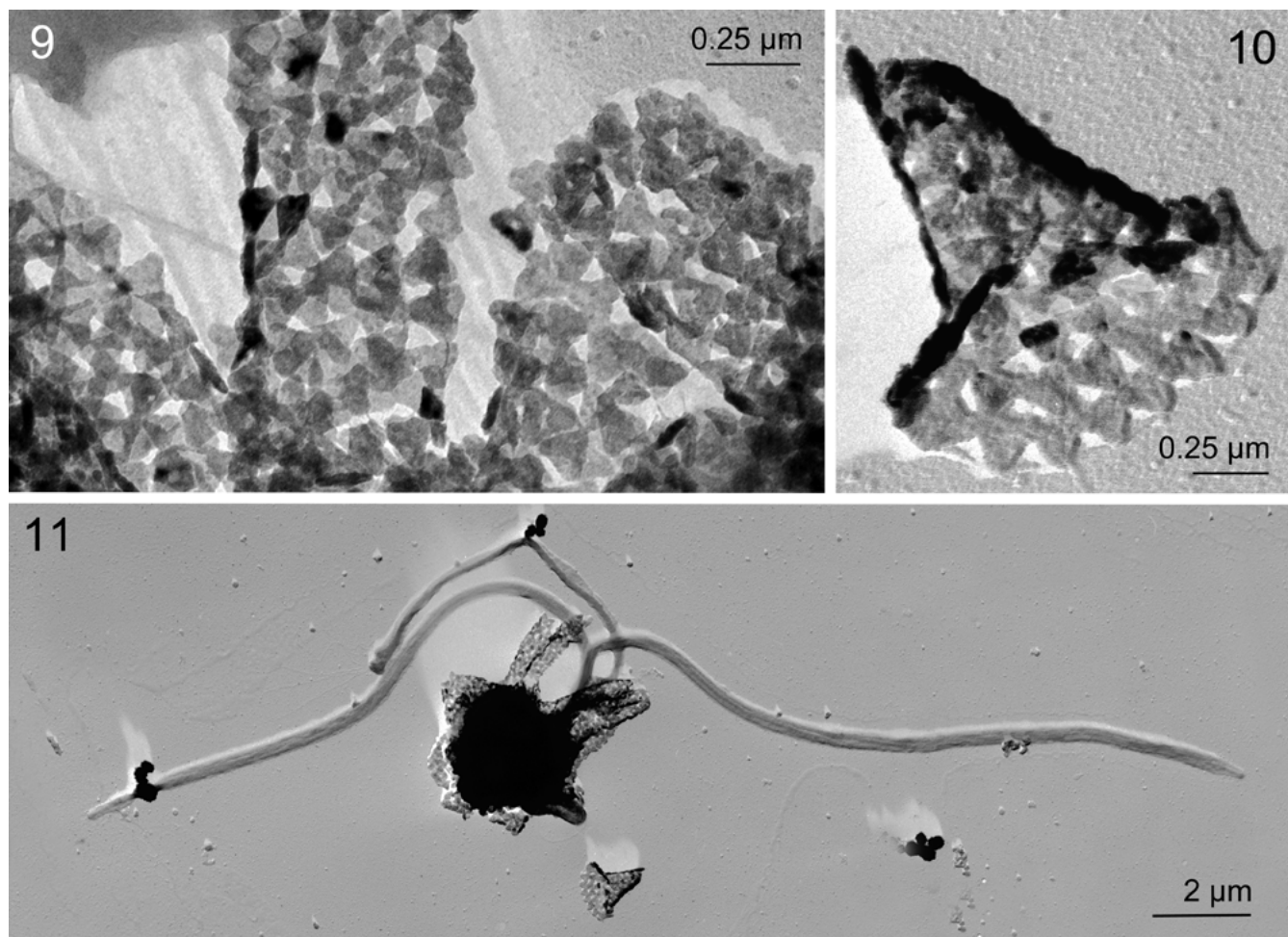
Table 2. Biogeographical data for species of *Pappomonas* and *Trigonaspis*. The question mark in front of *T. minutissima* and *T. melvillea* refers to the lack of formal evidence linking these taxa with *P. borealis* and *P. weddellensis* respectively. Type localities are indicated by using bold face.

Hemisphere	Northern hemisphere										Southern hemisphere			
Region	Arctic					Non-Arctic					Antarctica			
Locality	W. Greenland (Disko)	North East Water Polynya (NEW)	Svalbard	Homer, S. Alaska	Norway	Denmark	Finland	California, Monterey Bay	Mexico, Sea of Cortez		Cape Town, S. Africa	Weddell Sea (Ameritz)	Weddell Sea (EPOS)	Weddell Sea (ANTX73)
<i>Pappomonas/Trigonaspis</i>														
<i>P. flabellifera</i> (S. Afr. type mat.)								17						
<i>P. flabellifera</i> (main morphotype)	7,10,13,14	19	19		9	8			17		1			
? <i>T. minutissima</i>	6,13,14					8								
<i>P. borealis</i>	1,3,7,10,13,14	19	19	3		8								
<i>T. diskoensis</i>	6,10,13,14				9	8								
<i>P. weddellensis</i>											11	19	19	18
? <i>T. melvillea</i>											11	20	20	
<i>P. garrisonii</i>													19	
<i>P. garrisonii</i> HOL (= <i>T. sp.</i>)											20	20	20	
<i>Balaniger</i>														
<i>B. virgulosa</i> HET (syn. <i>Pap. virgulosa</i>)	2,7,10,13,14	19		3	9	8	5,15,21							
<i>B. virgulosa</i> HOL (syn. <i>Bal. balticus</i>)	7	19				4,21	5,12,15,16,21							

1) Manton and Oates 1975
2) Manton and Sutherland 1975
3) Manton *et al.* 1976a
4) Thomsen and Oates 1978
5) Thomsen 1979
6) Thomsen 1980a
7) Thomsen 1981

8) Christensen *et al.* 1985
9) Espeland and Thronsdén 1986
10) Hansen *et al.* 1988
11) Thomsen *et al.* 1988
12) Vørs 1992
13) Østergaard 1993
14) Clausen *et al.* 1994

15) Ikävalko and Thomsen 1997
16) Ikävalko 1998
17) Thomsen and Buck 1998
18) Findlay and Giraudeau 2000
19) Thomsen and Østergaard 2014b
20) This paper
21) Thomsen, unpublished



Figs 9–11. *Trigonaspis diskoensis*. TEM whole mounts from NE Greenland (NEW) (Fig. 9), and West Greenland (Arctic Station) (Figs 10–11). **9** – high magnification of tower-shaped flagellar pole coccoliths (from Fig. 5) showing the helical placement of triangular crystallite groups; **10** – high magnification of hat-shaped coccolith detached from the cell shown in Fig. 11. Notice that the triangular crystallites are arranged in highly organized tiers; **11** – Whole cell with extended flagella and haptonema.

turn of the helix in the narrowest middle part of the FPC involves only 4–5 triangles.

The 2D-matrix of triangles on the individual body coccolith (Fig. 14) appears in the undisturbed BC to be similarly well organized as previously reported for *T. diskoensis*.

In contrast to *T. diskoensis* there is in *T. minutissima* a slight difference in the size of triangles among flagellar pole and body coccoliths (see Table 1), with triangles from the body coccoliths being marginally larger.

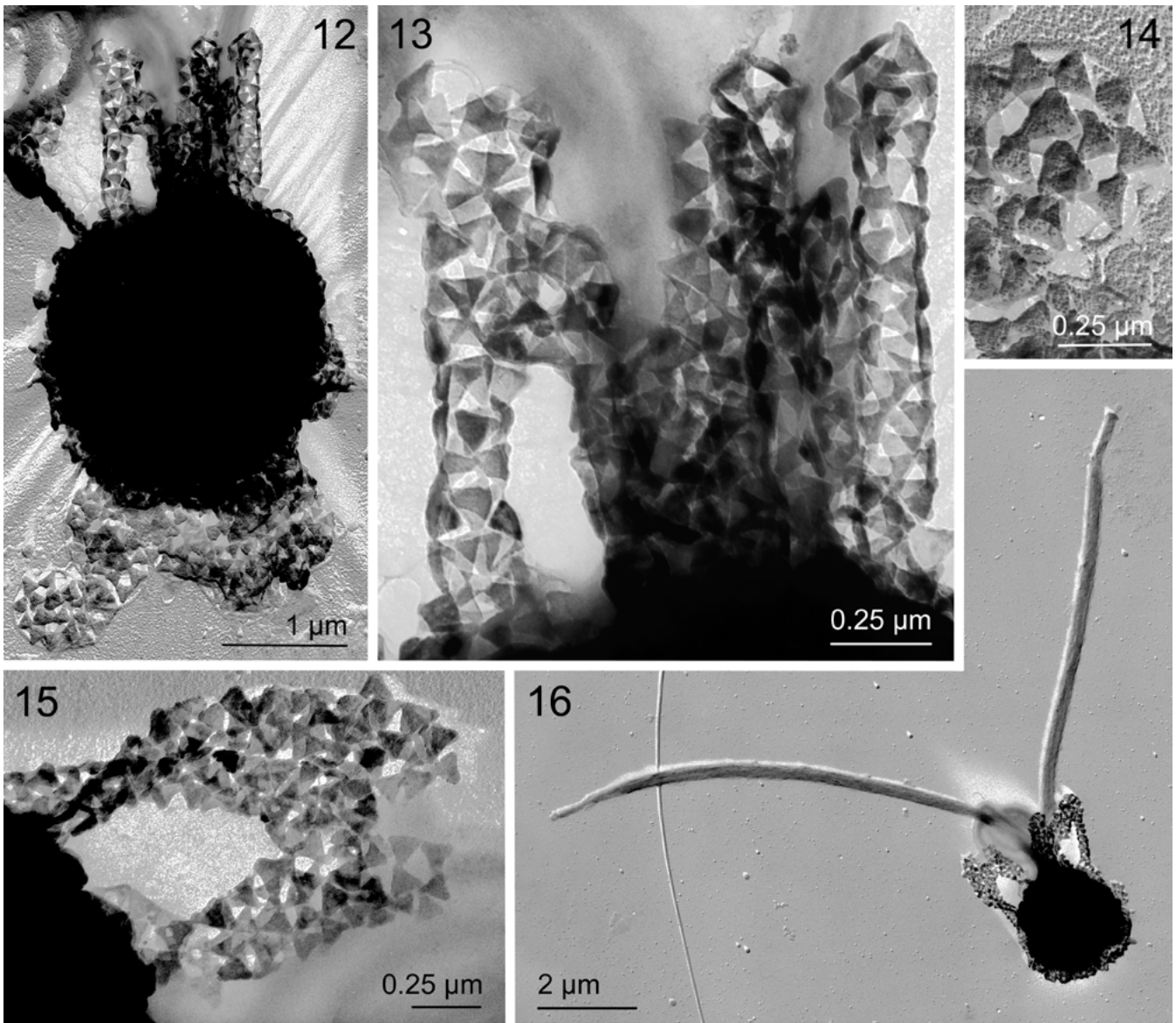
A life cycle counterpart of *T. minutissima* remains to be discovered. Considering the convincing similarity between *T. diskoensis* and *T. minutissima* in all crucial morphological features, the life cycle counterpart

is likely to be a species of *Pappomonas*. *Pappomonas flabellifera* Manton and Oates 1975 which is also abundantly present in the Disko Bay area (Thomsen and Østergaard 2014b) is from all perspectives a strong candidate.

Biogeographical data on *T. minutissima* is presented in Table 2.

***Trigonaspis melvillea* Thomsen in Thomsen *et al.* 1988**

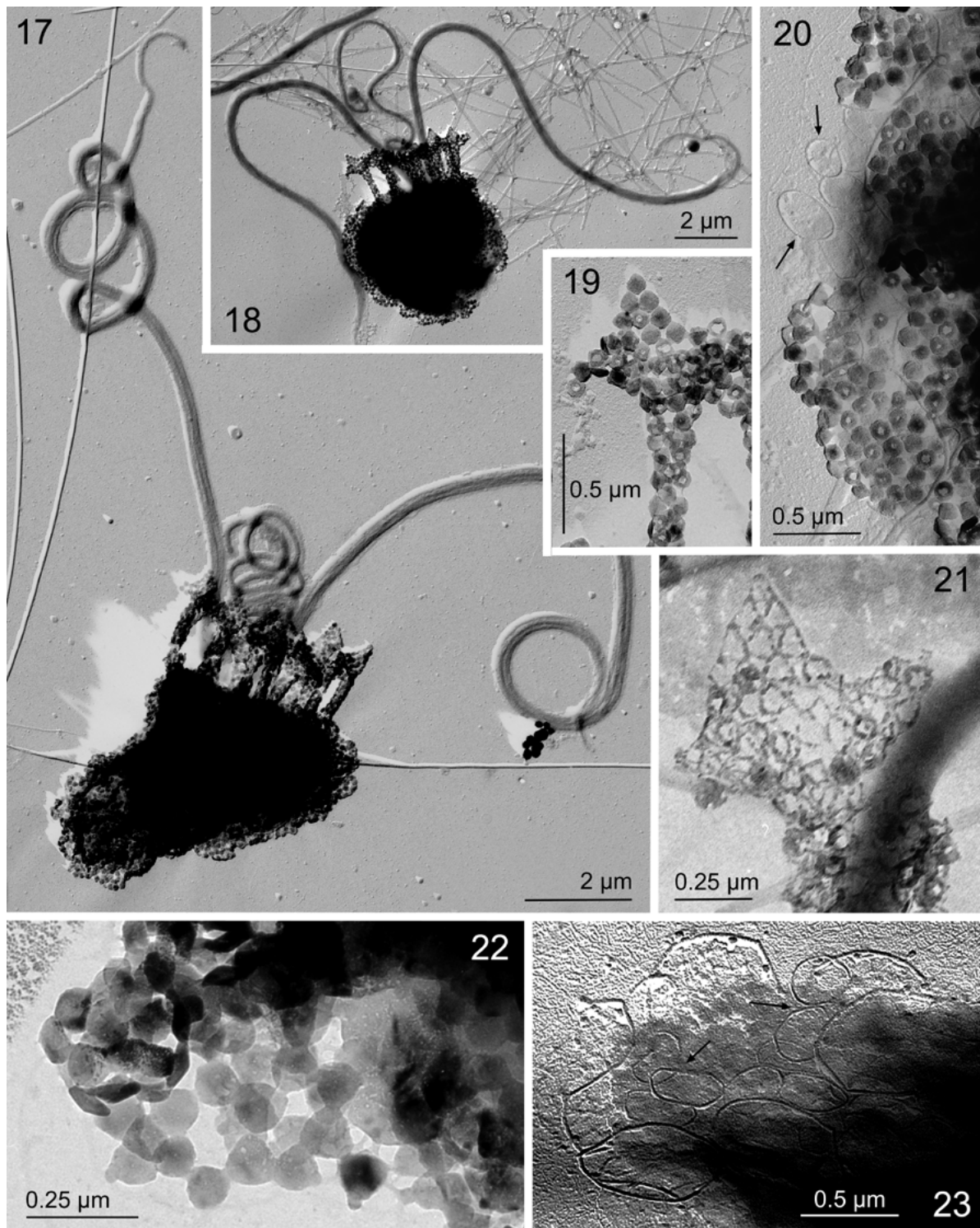
This taxon was first described from the Weddell Sea, Antarctica, based on material from the AMERIEZ cruise (Thomsen *et al.* 1988). The species is here re-examined based on supplementing Antarctic material (EPOS and ANT X/3).



Figs 12–16. *Trigonaspis minutissima*. TEM whole mounts from West Greenland (Arctic Station). **12** – whole cell with partly detached coccoliths; **13** – detail from Fig. 12 of flagellar pole coccoliths showing triangular crystallite groups and slender towers wreathed with 4–5 of these in a random transect; **14** – detail of body coccolith from the cell shown in Fig. 12; **15** – detail of coccoliths from the cell shown in Fig. 16; **16** – whole cell with flagella and curled up haptoneuma.

The appearance of the cell emphasizing appendages (flagella and haptoneuma) and the overall layout of the coccolith coverage is accounted for in Figs 17 and 18. Numerical facts have been assembled in Table 1. *Trigonaspis melvillea* has dimorphic coccoliths, viz. a tuft of highly distinct spear-shaped flagellar pole coccoliths, and oval, disc-shaped body coccoliths elsewhere. Both types of coccoliths are in accordance with the *Trigonaspis* genus concept covered by triangular plates of

crystallites. Whereas the triangles of both *T. diskoensis* and *T. minutissima* are generally found to have either a straight or a slightly concave edge, the situation is different in *T. melvillea* where most triangles have slightly convex edges which endows the individual triangle with a roundish appearance (Figs 19, 20, 22). However, when examining e.g. a decalcified specimen, as illustrated in Fig. 21, it is very evident from the organic matrix remaining, that the basic geometry is a distinct tri-



Figs 17–23. *Trigonaspis melvillea*. TEM whole mounts from the Weddell Sea, Antarctica. **17** – whole cell with flagella and a curled up haptonema positioned inside a corona of distinct flagellar pole coccoliths; **18** – complete cell with flagella and partly extended haptonema; **19** – detail of the distal termination of a flagellar pole coccolith (from Fig. 18); **20** – rimmed body coccoliths supporting densely packed layers of crystallite groups (from Fig. 18). Unmineralized under layer scales are pointed out; **21** – detail of unmineralized termination of flagellar pole coccolith. The still remaining organic matrix clearly reveals the triangular shape of a crystallite group; **22** – detail of body coccolith calcification. Notice that the triangles are united to form hexagonal rings; **23** – uncalcified specimen showing body coccolith base plates and under layer scales (arrows).

angular shape. The triangle edge length in *T. melvillea* is markedly smaller than observed in both *T. diskoensis* and *T. minutissima* (see Table 1). The organization of triangles in the FPC is strictly pyramidal when examining the distal spear-shaped termination of the coccolith, while the shaft seems to be carrying triangles organized in the same helical pattern that has previously been described for both *T. diskoensis* and *T. minutissima*. The organization of triangles on a BC deviates in *T. melvillea* from the concentric and closely abutted layout that characterizes both *T. diskoensis* and *T. minutissima*. In *T. melvillea* the triangles are thus organized in an open mesh structure comprising interwoven pentagonal (see Thomsen *et al.* 1988, l.c. Fig. 29) or hexagonal rings (Fig. 22). Unmineralized under layer scales are frequently observed (e.g. Figs 20 and 23).

So far there is no evidence for life history events implicating a phase shift between the holococcolithophorid *T. melvillea* and a species from the heterococcolithophorid genus *Pappomonas*. Two candidate species of *Pappomonas* occur (Thomsen and Østergaard 2014b) within the geographic realm of *T. melvillea*, viz. *P. weddellensis* Thomsen in Thomsen *et al.* 1988 and *P. garrisonii* Thomsen and Østergaard 2014b. It is argued below that *P. garrisonii* enters into a shared life history with an undescribed *Trigonaspis* sp. that deviates markedly from *T. melvillea*, thus leaving *P. weddellensis* as a strong candidate for sharing a life history with *T. melvillea*.

Biogeographical data on *T. melvillea* is presented in Table 2.

***Trigonaspis* sp. (= *Pappomonas garrisonii* (HOL) Thomsen and Østergaard 2014b)**

A new species of *Trigonaspis* was encountered in AMERIEZ, EPOS and ANT X/3 samples from the Weddell Sea, Antarctica. A complete cell with flagella and haptonema is shown in Fig. 24. The tower-shaped coccoliths are present on the entire cell surface and most prominently developed at the flagellar pole. In terms of general appearance of the tower-shaped coccoliths (Fig. 25) it is obvious that these are very reminiscent of those of *T. minutissima* (Fig. 13). Body coccoliths are rarely observed. However, we believe that the coccolith pointed out in Figs 25 represents a disc shaped body coccolith. The shape of the individual triangle (rounded corners and concave edges) is very similar to what has been described for *T. diskoensis* and *T. minutissima*. However, the *Trigonaspis* sp. triangles

are somewhat larger than those found in both *T. diskoensis* and *T. minutissima* (see Table 1).

Circumstantial evidence exists that links *Trigonaspis* sp. with *Pappomonas garrisonii* Thomsen and Østergaard 2014b. It is obvious from the documentation provided in terms of combination cells (see Thomsen and Østergaard 2014b; l.c. Figs 43–45) that the *Trigonaspis* counterpart of *P. garrisonii* possesses tower-shaped coccoliths very reminiscent of those described here for *Trigonaspis* sp., and it is furthermore evident that the size of the triangles also matches those of *Trigonaspis* sp. in overall size (see Table 1) and appearance.

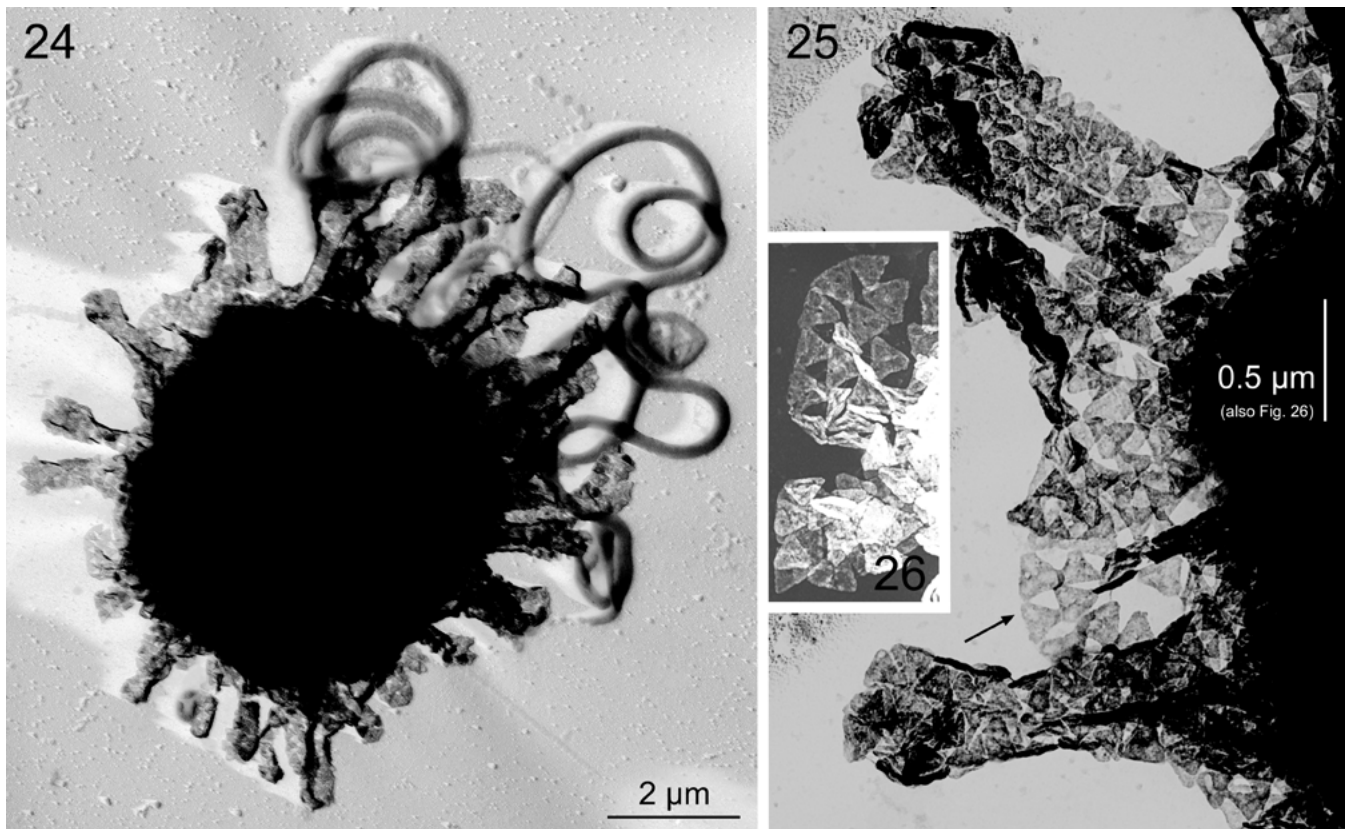
Due to the overarching possibility that *Trigonaspis* sp. is in fact the life history counterpart of *P. garrisonii* we have refrained from formally describing the species. We recommend that this taxon is in the future referred to informally as *P. garrisonii* HOL.

Biogeographical data on *P. garrisonii* HOL is presented in Table 2.

DISCUSSION

The reexamination of *T. diskoensis*, *T. minutissima* and *T. melvillea* drawing upon material from a more extended geographic coverage has in all details corroborated the original description of the species in question.

Two species of *Trigonaspis* are found in each hemisphere (Table 2). The genus *Trigonaspis* thus biogeographically and phylogenetically corroborates the general picture emerging with regard to the lightly calcified coccolithophorids of generic bipolarity coupled with a more restricted and unipolar distributional pattern at the specific level. The geographic realm of all taxa here examined is still rather limited. However, at least the persistent occurrence of all taxa at specific sites, viz. Disko Bay, W. Greenland, for the northern species and the Weddell Sea for the southern species deserves to be emphasized. It is obvious from the occurrence data assembled in Table 2 that the circumstantially evidenced life history pairs of taxa, viz. *P. borealis*/*T. diskoensis* and *P. garrisonii*/*T. sp.* have clearly overlapping geographical ranges. This applies as well to the life history pairs of taxa hypothesized here, viz. *P. flabellifera*/*T. arctica* and *P. weddellensis*/*T. melvillea*. Both *T. diskoensis* and *T. minutissima* have been recorded sparingly at non-arctic sites (Table 2), however, on all occasions at temperatures that mirror those from genuine arctic sites.



Figs 24–26. *Trigonaspis* sp. (= *Pappomonas garrisonii* HOL?). TEM whole mounts from the Weddell Sea, Antarctica. **24** – whole cell with curled up flagella and haptonema. Tower-shaped but differently sized coccoliths occur over the entire surface of the cell; **25** – detail (from Fig. 24) of tower-shaped coccoliths showing the triangular crystallite groups. Arrow points to a body coccolith; **26** – part of body coccolith calcification. Reversed printing.

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